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Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests

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Running head: Plant phylodiversity affects arthropods

Abstract

Global change is predicted to cause non-random species loss in plant communities, with consequences for ecosystem functioning. However, beyond the simple effects of plant species richness, little is known about how plant diversity and its loss influence higher trophic levels, which are crucial to the functioning of many species-rich ecosystems. We analyzed to what extent woody plant phylogenetic diversity and species richness contribute to explaining the biomass and abundance of herbivorous and predatory arthropods in a species-rich forest in subtropical China. The biomass and abundance of leaf-chewing herbivores, and the biomass dispersion of herbivores within plots, increased with woody plant phylogenetic diversity. Woody plant species richness had much weaker effects on arthropods, but interacted with plant phylogenetic diversity to negatively affect the ratio of predator to herbivore biomass. Overall, our results point to a strong bottom-up control of functionally important herbivores mediated particularly by plant phylogenetic diversity, but do not support the general expectation that top-down predator effects increase with plant diversity. The observed effects appear to be driven primarily by increasing resource diversity rather than diversity-dependent primary productivity, as the latter did not affect arthropods. The strong effects of plant phylogenetic diversity and the overall weaker effects of plant species richness show that the diversity-dependence of ecosystem processes and interactions across trophic levels can depend fundamentally on non-random species associations. This has important implications for the regulation of ecosystem functions via trophic interaction pathways and for the way species loss may impact these pathways in species-rich forests.

Keywords: BEF China; biodiversity; ecosystem function; herbivores; predators; species richness; trophic interactions

Introduction

The diversity of life on earth strongly influences the dynamics and properties of ecosystems, and global change-induced biodiversity loss may thus significantly alter ecosystem functioning and service provisioning (Hooper et al. 2012; Naeem et al. 2012). Most notably, plant species loss has been shown to negatively affect a wide range of ecosystem functions, such as biomass production and carbon sequestration (Cardinale et al. 2011; Cardinale et al. 2012). However, recent work has also indicated that plant species richness impacts on the abundance and diversity of higher trophic levels (e.g. Unsicker et al. 2006; Haddad et al. 2009; Sobek et al. 2009b; Scherber et al. 2010). This has important ecological consequences, as diversity-dependent effects on herbivores and predators can feed back on the producer level and strongly mediate biodiversity-ecosystem function relationships under real-world conditions (Haddad et al. 2009; Schuldt et al. 2010).

However, we are far from having a general understanding of such diversity-dependent trophic interaction effects (see also Cardinale et al. 2011), as even basic relationships between plant diversity and the diversity or abundance of herbivores and predators often seem not to show a consistent pattern (Koricheva et al. 2000; Vehviläinen et al. 2007; Sobek et al. 2009a; Castagneyrol and Jactel 2012; Schuldt et al. 2014b). While such inconsistent patterns potentially indicate relevant biological differences among systems, their interpretation is complicated by two important aspects. First of all, many studies are biased toward analyzing relatively species-poor and often simplified plant communities, in which it may be difficult to distinguish the effects of community composition from diversity effects (Nadrowski et al. 2010). Extrapolating to more diverse systems is hardly possible. Yet, information on species-rich systems may be particularly crucial, as diversity-dependent interactions between plants and higher trophic levels can play a key role in the functioning of such systems (e.g. Terborgh 2012). Secondly, most studies have focused on the effects of plant species richness as a very basic measure of biodiversity. However, relationships with herbivores or predators might be

72 more complex and not necessarily captured well by plant species richness alone. Plant species
73 loss in natural communities often occurs, and may cascade to affect higher trophic levels, in a
74 non-random way (Srivastava and Vellend 2005; Thebault et al. 2007; Cavender-Bares et al.
75 2009). Species may get lost in a phylogenetically structured manner that reflects
76 phylogenetically conserved functional adaptations to their biotic and abiotic environments,
77 such as the phylogenetically structured host selection of many consumers (e.g. Weiblen et al.
78 2006). This could explain why, even in plant species-rich systems, plant community
79 composition was repeatedly found to be a better predictor of herbivore and predator
80 assemblage structure than species richness (Perner et al. 2005; Rzanny et al. 2013). Measures
81 of diversity that incorporate the relatedness among species in terms of evolutionary and
82 functional similarity may thus substantially improve our understanding of diversity
83 relationships across trophic levels (Dinnage et al. 2012; Pellissier et al. 2013).
84 Plant phylogenetic diversity qualifies as a particularly comprehensive predictor in this
85 respect, as it may not only account for complex functional trait interactions that affect higher
86 trophic levels (if key functional traits are phylogenetically conserved; Cavender-Bares et al.
87 2009; Srivastava et al. 2012), but can also indicate the effects of shared evolutionary and
88 biogeographic history among species (Futuyma and Agrawal 2009; Pellissier et al. 2013).
89 Dinnage et al. (2012) recently showed in a grassland experiment that plant phylogenetic
90 diversity strongly interacted with plant species richness to affect arthropod diversity, with
91 effects of plant species richness becoming stronger at high levels of plant phylogenetic
92 diversity. For natural systems, however, where processes of non-random community assembly
93 may strongly affect the phylogenetic structure of plant and animal communities, the effects of
94 phylogenetic diversity on arthropods remain poorly explored. This applies particularly to
95 species-rich subtropical and tropical forests, where arthropods play an important role in
96 maintaining the high tree diversity and may contribute to structuring plant phylogenetic
97 community composition (Cavender-Bares et al. 2009; Paine et al. 2012; Terborgh 2012).

98 Here, we analyze to what extent the phylogenetic diversity and species richness of
99 woody plants contribute to explaining the biomass and abundance of herbivorous and
100 predatory arthropods along gradients of woody plant species richness and stand age in a
101 highly diverse subtropical forest in China. Biomass, in particular, is directly related to the
102 functional impact of consumers (Saint-Germain et al. 2007; Reiss et al. 2011), but its
103 relationship with plant diversity in such highly diverse forests is poorly understood (and the
104 same even applies to the more frequently studied abundance of arthropods; Whitfeld et al.
105 2012). We focus on the overall biomass and abundance of predators, leaf chewing herbivores
106 and sucking herbivores, which allows us to obtain insight into the net ecosystem effect of key
107 functional groups in this system. In addition, we test for diversity effects on the variability in
108 biomass distributions among individuals in each of our 27 study plots, which might be related
109 to the degree of resource differentiation in arthropod assemblages (Rudolf 2012).
110 Plant diversity might have a direct effect on herbivore and predator assemblages via
111 increased and more stable resource diversity, with positive effects on generalist herbivores
112 and predators (the 'dietary-mixing' and 'enemies' hypotheses; Root 1973; Haddad et al. 2009;
113 Dinnage 2013) and negative effects on specialized herbivores (the 'resource-concentration'
114 hypothesis; Root 1973; but see Plath et al. 2012). It might also promote consumers indirectly
115 via diversity-dependent effects of plant productivity on consumer biomass (the 'more-
116 individuals' hypothesis; Srivastava and Lawton 1998). We hypothesize that (i) the biomass
117 (and its variability within study plots) and abundances of both herbivores and predators
118 increase with woody plant diversity in our study system. Specifically, we expect that (ii)
119 changes in biomass and abundance are better predicted by plant phylogenetic diversity than
120 plant species richness, as phylogenetic diversity better explains the complexity of
121 evolutionary and functional characteristics that may underlie diversity effects. As woody plant
122 diversity in our study plots has been found to increase primary productivity (Baruffol et al.
123 2013), we include alternative analyses that substitute productivity data for diversity metrics to

test whether (iii) resource diversity or plant primary productivity underlie potential diversity effects. As support for both the resource diversity and productivity mechanism has been controversial, even for the much better studied grassland systems (Haddad et al. 2009; Borer et al. 2012), knowledge of these potential impacts of these mechanisms on herbivores and predators in highly diverse forests will advance our general understanding of the community-level consequences of changes in biodiversity.

Materials and methods

Study site and plot design

The study was conducted in the Gutianshan National Nature Reserve (29°14´ N; 118°07´E) in Zhejiang province, south-east China. The reserve covers 8000 ha of evergreen mixed broadleaved forest on a sloping terrain (300-1260 m a.s.l.). In the reserve, about 1430 seed plant species, 260 of them woody, have been recorded (Legendre et al. 2009; Bruelheide et al. 2011). The subtropical monsoon climate is characterized by a mean annual temperature of 15.3°C and a mean annual precipitation of about 2000 mm (Hu and Yu 2008), with most of the rainfall occurring in May and June (Geißler et al. 2012).

As part of the BEF (Biodiversity and Ecosystem Functioning) China project (www.bef-china.de), 27 study plots of 30 x 30 m were established in 2008, which were randomly spread (as far as logistically feasible; distance among plots was on average 2.6 km ± 2.3 *SD* (range 0.1 - 8.6 km)) across the reserve. Plot selection followed a stratified sampling design based on woody plant species richness (25-69 species per plot) and stand age (with < 20 to > 80 years since the last logging events, or, in some cases, since agricultural activities). Details of plot selection and plot characteristics (including data on the plant species composition of all 27 plots) are given in Bruelheide et al. (2011).

Arthropod sampling

Arthropods were sampled at three time periods to capture seasonal patterns in the herbivore assemblages, i.e. September/October 2011 (toward the end of the growing season), April 2012 (before the rainy season, after the start of the growing season) and June 2012 (at the end of the rainy season, peak of the growing season). We used a beating technique that allows for a direct assessment of arthropods at the level of individual trees (Ødegaard et al. 2005; Campos et al. 2006; Wardhaugh et al. 2012). Arthropods were knocked down from 25 tree and shrub saplings onto a beating sheet (70 cm diameter). Saplings were selected every two meters along a transect running diagonally through the plot. The composition of these 25 randomly selected saplings very well mirrored the differences in the community composition among plots of the overall woody plant communities (Procrustes correlation = 0.90; $P < 0.001$; see Methods in Electronic Supplementary Material (ESM)). Sapling species identity was determined with the help of local experts. The height of each sampled sapling was recorded in the field. Mean height was 1.77 m, with a SD of 0.48 m, indicating that a similar volume of plant structures was sampled from above the beating sheet for most individuals (see also Campos et al. 2006). However, to account for potential effects of tree height on arthropod samples, individual sapling height was included as a covariate in the statistical analyses. Transect lines varied between the fall and spring surveys, thus sampling a different set of tree and shrub individuals, but were identical between the spring and summer surveys for logistical reasons.

Arthropods were sorted to higher taxa (basically order level, but with further distinctions in orders such as Coleoptera, Hymenoptera, Hemiptera, to distinguish predators and different herbivore guilds; see Table S1 in ESM for details) and classified as (mainly) predators or herbivores (following the classification of Novotny et al. 2010 and using morphological characteristics such as mandible shapes where necessary). For the herbivores, we distinguished between leaf chewers and sap suckers; other herbivore guilds were too rare for separate analysis. As our main focus was on overall biomass and abundance patterns, we

did not sort arthropods to (morpho)species, which can be challenging and error-prone for highly diverse taxa (e.g. many juvenile spiders and lepidopteran caterpillars; e.g. Strutzenberger et al. 2011). Biomass and abundance patterns are particularly important in determining the functional impact of primary and secondary consumers (Saint-Germain et al. 2007; Reiss et al. 2011), and many studies have shown that overall patterns at the level of important functional groups can be highly informative for our understanding of the regulation of ecosystem functions in light of changing plant diversity (Perner et al. 2005; Vehviläinen et al. 2007; Vehviläinen et al. 2008; Haddad et al. 2009; Borer et al. 2012; Whitfeld et al. 2012). For all predatory and herbivorous arthropods, body length (excluding body appendages such as ovipositors and antennae) was measured to the closest 0.1 mm under a stereomicroscope with a built-in micrometer gauge. Biomass for each sampled individual was estimated on the basis of taxon-specific body length-biomass equations of Hódar (1996) and Wardhaugh (2013).

Environmental data

Woody plant species richness for each plot was based on a complete inventory of all tree and shrub individuals > 1 m height, measured at the time of plot establishment in 2008. Data for the calculation of the phylogenetic diversity of the woody plant communities (see statistics) was obtained from an ultrametric phylogenetic tree of all angiosperm woody species recorded in the 27 study plots (Purschke et al. 2014). The tree was based on rbcL and matK sequences of the species (downloaded from NCBI Genbank; http://www.ncbi.nlm.nih.gov), which were aligned in Bioedit and processed in MEGA5 (Tamura et al. 2011) to obtain a phylogenetic tree based on maximum likelihood (ML). The ultrametric tree was computed from the ML topology using penalized likelihood, with branch lengths indicating divergence time.

Plot age was estimated from tree stem cores and diameter at breast height measurements (to the closest 0.1 mm) (Bruelheide et al. 2011). Plot age was correlated with,

and used as a comprehensive measure of, plot characteristics that change with succession, such as canopy cover (Pearson's r = 0.72; P < 0.001 for the correlation with plot age) and total basal area of woody plants (r = 0.76; P < 0.001) (see Schuldt et al. 2010). We also accounted for the topographic variability of our study site, which may further affect environmental plot conditions, by including the elevation (m) of the plots in our analyses.

Plot-level primary productivity over a two year period was inferred from tree growth data in 2008 and 2010. Basal area increments of all trees > 10 cm diameter at breast height, assessed with permanent dendrometer bands or with measuring tapes, were calculated and used as a proxy for relative tree growth (see Baruffol et al. 2013 for details). As a number of trees were destroyed in two plots due to illegal harvesting before measurements in 2010, productivity data was only available for 25 plots.

Statistical analysis

Woody plant phylogenetic diversity (Q_{phyl}) was calculated as the abundance-weighted version of Rao's quadratic entropy Q (Botta-Dukát 2005). Q_{phyl} was not completely independent of woody plant species richness (r = 0.48; P = 0.011) and plot age (r = 0.57; P = 0.002). As a metric of phylogenetic diversity that reflects the extent to which woody plant communities are phylogenetically more clustered or overdispersed than expected by chance, we thus calculated standardized effect sizes of Q_{phyl} (Q_{phyl} s.e.s.) based on the null model '1s' in Hardy et al. (2008). These s.e.s. values are independent of a given plant community's species richness (r = -0.26; P = 0.186 in our study). In our case, they were also unrelated to plot age (r = -0.01; P = 0.959). Standardized effect sizes were calculated as the observed phylogenetic diversity relative to expected values from the random communities: ses = (observed phylogenetic diversity index score – mean expected index score)/standard deviation of the index (Gotelli and Rohde 2002).

Based on Rao's Q, we also quantified the functional dispersion of the biomass of all

leaf chewer, sap sucker or predator individuals per plot and sampling time (Q_{Bio}). Higher values of Q_{Bio} indicate larger biomass dissimilarity of the individuals of a given group within a study plot, which may point to higher resource differentiation among individuals (Schleuter et al. 2010). Q_{Bio} was not dependent on the number of individuals in a given plot (chewers: r = -0.07; P = 0.564; suckers: r = -0.01; P = 0.913; predators: r = -0.19; P = 0.084). Calculations of Rao's Q were based on standardized variables (mean = 0, SD = 1) and a Euclidean species distance matrix. All continuous predictors (i.e. all variables except sampling time) were standardized prior to the analysis. Correlations among predictors (all with an $r \leq 0.57$) indicated that none of the predictors were highly collinear. The mean biomass and abundances of leaf-chewing herbivores, sap-sucking herbivores, predatory arthropods, and the predator-herbivore biomass and abundance ratios per plot and sampling time—as well as the functional dispersion (Q_{Bio}) of leaf chewer, sucker and predator biomass—were used as response variables. Arthropod biomass and abundance values were averaged for each of the three sampling times across the 25 saplings sampled per plot as different tree and shrub individuals were included in the three different sampling campaigns (see above). Linear mixed effects models were used to account for potential effects of temporal or spatial pseudoreplication. Plot identity was included as a random effect. We also tested for a random interaction effect of sampling time and plot identity, but likelihood ratio tests indicated that this term was not significant and could be dropped. As fixed effects, we included sampling time, elevation, sapling height, plot age, woody plant species richness, woody plant phylogenetic diversity (standardized effect sizes Q_{phyl} s.e.s), as well as all two-way interactions between sampling time, plot age, species richness and phylogenetic diversity. The number of woody plant species sampled in a plot had no effect on any of the response variables and was not included in the models. The response variables and woody plant species richness were log-transformed to improve model fit. The full models with all predictors (i.e. in the form of: response ~ sampling time + elevation + sapling height + plot age + woody plant species richness +

254 woody plant phylogenetic diversity (Q_{phyl} s.e.s.) + time:age + time:richness +
255 time:phylodiversity + age:richness + age:phylodiversity + richness:phylodiversity ,
256 random=~1|plot) were simplified by excluding predictor variables in an automated stepwise
257 procedure based on the AICc (Burnham and Anderson 2004) and maximum likelihood
258 estimation. The models with the smallest number of predictors and the lowest global AICc
259 were chosen as the most parsimonious, best-fit models for each response variable. Model
260 residuals were checked for normality and homogeneity of variances. To assess whether
261 potential effects of tree diversity could be explained by plot-level primary productivity, we re-
262 ran all analyses that indicated diversity effects in the minimal models, replacing the measures
263 of diversity (woody plant species richness and phylogenetic diversity) by plot-level
264 productivity data. Productivity in the study plots was previously found to be strongly related
265 to woody plant species and phylogenetic diversity (Baruffol et al. 2013) and, to avoid
266 statistical biases due to collinearity and to keep model complexity to an acceptable level, we
267 did not directly include productivity in the models which tested for diversity effects. All
268 analyses were conducted in R 3.1.0 (http://www.R-project.org) with the packages *picante*
269 (Pinheiro et al. 2014) and *nlme* (Kembel et al. 2010).
270
271 **Results**
272 In total, we recorded 6950 arthropods with a total biomass of 29,167 mg across the three
273 sampling periods. Predators were most abundant (4737 individuals; 79% spiders), followed by
274 leaf-chewing herbivores (1282 individuals; 41% lepidopteran caterpillars, 32% orthopterans)
275 and sap-suckers (931 individuals; 74% Auchenorrhyncha). However, biomass was higher for
276 leaf chewers (16,730 mg; 42% orthopterans, 37% lepidopteran caterpillars) than for predators
277 (9387 mg; 66% spiders) and sap suckers (3050 mg; 82% Auchenorrhyncha). Biomass and
278 abundance correlated particularly strongly for sap suckers (Pearson's $r = 0.74$; $P < 0.001$) but
279 less so for predators ($r = 0.38$; $P < 0.001$) and leaf chewers ($r = 0.37$; $P < 0.001$). Predator and

herbivore biomass were not significantly correlated (P > 0.80 in all cases). In contrast, predator abundance was positively related to leaf chewer abundance (β = 0.26 ± 0.09 *SE*; t = 2.85; P = 0.006 for log-transformed abundance values in a mixed model including sampling time as a covariate) and tended to slightly increase with the abundance of sap suckers (β = 0.07 ± 0.05 *SE*; t = 1.37; P = 0.175).

In general, mixed models for both biomass and abundance pointed to similar variables affecting patterns within the predator and the two herbivore groups across the 27 study plots. However, diversity effects were always more pronounced for biomass as compared to mere abundance patterns (Table 1, Table S2). Thus, in the following we focus on biomass patterns (see Table S2 in ESM for abundance patterns). Leaf chewer biomass was particularly strongly affected by, and increased with, woody plant phylogenetic diversity (Q_{phyl} s.e.s.) (Table 1, Fig. 1a). Leaf chewer biomass further tended to increase with woody plant species richness, but this effect was not significant (P = 0.07; Table 1). In contrast to leaf chewers, sap-sucking herbivores were not affected by plant phylogenetic diversity, showing only a response to sampling period (Table 1). Likewise, the biomass of predators was not related to plant phylogenetic diversity, but increased with plot age (Fig. 1b). In contrast, the ratio of predator to herbivore biomass was strongly affected by the interaction between woody plant phylogenetic diversity and plant species richness (a pattern that was not detectable with mere abundance data; Table S2). The ratio of predators to herbivores was highest in plant species-poor plots with lower than expected phylogenetic diversity and strongly decreased with increasing plant phylogenetic diversity and plant species richness (Fig. 1c).

The dissimilarity in biomass among leaf chewer individuals within plots—measured as biomass dispersion Q_{Bio}—was lowest in plant species-poor plots with lower than expected phylogenetic diversity and strongly increased with both woody plant phylogenetic diversity (Q_{phyl} s.e.s.) and plant species richness (Table 2, Fig. 2). Sap sucker biomass dispersion

showed a response to plant phylogenetic diversity only during summer (Time 3; Table 2). Biomass dispersion among predators was not related to plant phlogenetic diversity, but decreased with woody plant species richness (only significant at Time 2; Table 2).

The effects of plant phylogenetic diversity on leaf chewing herbivores and the predator-herbivore ratio were also evident when observed plant phylogenetic diversity instead of standardized effect sizes were analyzed (however, with changes in the roles of plot age and plant species richness due to the correlation of these variables with observed phylogenetic diversity; Tables S5 and S6, Fig. S1).

Plot-level primary productivity did not underlie the effects of plant phylogenetic diversity on arthropods. Plant productivity was not retained in any of the minimal models when the analyses showing significant effects of Q_{phyl} s.e.s. were re-run with measures of woody plant diversity replaced by plant productivity (Tables S3 and S4).

Discussion

Our study highlights how effects of plant diversity that go beyond simple effects of increasing species numbers contribute to controlling consumer biomass across trophic levels in a highly diverse forest. Leaf chewer biomass and the biomass dispersion of herbivores strongly increased across forest stands with increasing plant phylogenetic diversity. In contrast, effects of woody plant species richness were less frequent and less pronounced, interacting with plant phylogenetic diversity to affect arthropods in some cases. Overall, our results indicate a strong bottom-up control of functionally important herbivores mediated by woody plant phylogenetic diversity, and they show no sign of the increase in top-down effects of predator biomass or abundance generally expected to occur with increasing plant diversity (Root 1973; Haddad et al. 2009). Our findings have important implications for the regulation of ecosystem functions via trophic interaction pathways in these species-rich forests.

Plant species richness vs. phylogenetic diversity effects

While the comparatively weak direct influence of plant species richness on arthropod biomass and abundance in part contrasts with the findings from some other systems (mostly experimental grasslands; e.g. Haddad et al. 2009; Scherber et al. 2010), many other studies have likewise found no, or only weak and inconsistent, plant species richness effects (e.g. Koricheva et al. 2000; Perner et al. 2005; Vehviläinen et al. 2007; Vehviläinen et al. 2008). Interestingly, plant species richness effects are often considered to be mediated, and outperformed, by the influence of plant species composition (Perner et al. 2005; Zhang and Adams 2011; Rzanny et al. 2013). Metrics of plant diversity that account for the relatedness among species may thus help to reconcile contrasting findings by more effectively revealing the complexity of plant diversity effects beyond the mere impact of plant species richness (see Dinnage et al. 2012). This is demonstrated in our study, and for the first time for such species-rich forests, by the strong effects of woody plant phylogenetic diversity compared to overall weaker plant species richness effects. Many herbivores show phylogenetically structured host use (e.g. Weiblen et al. 2006), and phylodiversity-dependent patterns in herbivore assemblages might cascade to affect particularly specialized predators, whereas the response of generalist predators might be less pronounced. Thus, it is not surprising that the effect of woody plant phylogenetic diversity was particularly evident for herbivores and less so for predators, which in our case were largely generalist spiders. However, interactive effects of plant species richness and phylogenetic diversity on the predator to herbivore biomass ratio and on the biomass dispersion of leaf chewers indicate that species richness can contain information that is not fully captured by phylogenetic diversity, as can be the case when functionally important traits are not phylogenetically conserved (Srivastava et al. 2012; Schuldt et al. 2014b).

Leaf-chewing vs. sap-sucking herbivores

358 Leaf-chewing herbivores are responsible for the majority of visible leaf damage in the studied
359 forest (Schuldt et al. 2010; Schuldt et al. 2012), and they also represented the largest
360 proportion of the arthropod biomass in our samples (ca. 57% of the total and 85% of the
361 herbivore biomass). The increase in leaf chewer biomass and abundance with higher woody
362 plant phylogenetic diversity corresponds well to the increase in herbivore damage with
363 increasing woody plant diversity found previously on the same study plots (Schuldt et al.
364 2014a). These patterns strongly suggest that the functional impact of herbivores increases
365 with woody plant diversity. This contrasts with the general expectations of the resource-
366 concentration hypothesis (Root 1973; Haddad et al. 2009) and also with commonly held
367 assumptions that herbivores become increasingly specialized toward lower latitudes (Coley
368 and Barone 1996; Dyer et al. 2007). However, our previous studies provided strong
369 indications that the dominant herbivores in this system are generalists that may benefit from
370 higher resource diversity in the more plant-diverse forest stands (Schuldt et al. 2014a). This
371 mechanism, formulated by the 'dietary-mixing' hypothesis (Bernays et al. 1994; Dinnage
372 2013), and the probable dominance of generalist herbivores (which has also been suggested
373 for other species-rich forests; e.g. Novotny et al. 2012), may explain the observed positive
374 relationship between leaf chewer biomass and woody plant phylogenetic diversity. In
375 particular, if the defense or palatability traits most relevant for herbivores show phylogenetic
376 clustering, phylogenetically more diverse plant communities provide generalist herbivores
377 with alternative hosts that help overcome dietary limitations on herbivore performance
378 (Cavender-Bares et al. 2009; see Parker et al. 2012 for a real-world example). Leaf traits
379 potentially important to herbivores that were found (among a set of 21 species) to show a
380 phylogenetic signal at our study sites were e.g. dry matter content, toughness, polyphenols,
381 tannins, and carbon and nitrogen contents (Schuldt et al. 2012; Eichenberg et al. 2014).
382 Interactions among such traits and responses of individual herbivore species from the
383 multidiverse set of herbivores potentially attacking a given plant species may make the

functional response of plants highly complex, and our phylogenetic diversity metric might capture the overall response of herbivore assemblages by integrating over the evolutionary adaptations of these herbivores. Without doubt, however, plant functional traits need to be explicitly addressed to identify the mechanisms underlying the observed diversity effects, and traits might also provide additional information on variation in the arthropod data not explained in our current models (see also Schuldt et al. 2014a). For instance, the fact that in some cases we observed effects of woody plant species richness beyond those of plant phylogenetic diversity might be a signal of functional trait information that is not phylogenetically conserved. The multitude of chemical, morphological and physiological traits that might potentially play a role in affecting arthropods, and the complexity of potential relationships among traits, however, require an extensive trait dataset for further testing that is often not available for many study regions. Yet, we hope that the results of our study will help to motivate efforts to unveil the complexity behind trophic interactions that might be key for ecosystem functioning in many species-rich systems.

The assumption that resource-diversity effects and not an increase in plant productivity were underlying reasons for the effects of plant phylogenetic diversity is supported by two additional findings of our study. First of all, even though primary productivity was previously found to increase with woody plant diversity (Baruffol et al. 2013), in our study it was not significantly related to any of the arthropod biomass and abundance patterns that showed a relationship with woody plant phylogenetic diversity. While the impact of plant diversity on arthropods operating through an increase in plant biomass may be common (e.g. Borer et al. 2012), the strength of these effects can vary and they may be overruled by resource diversity effects (Perner et al. 2005; Haddad et al. 2009; Dinnage et al. 2012). Secondly, the biomass distribution of leaf chewers within plots (Q_{Bio}) became more diverse with increasing plant phylogenetic diversity and woody plant species richness, which might be indicative of increased niche separation among herbivores due to a more

410 heterogeneous resource distribution (Mason et al. 2005). This higher biomass diversity, in
411 turn, may contribute to strengthening the previously observed top-down effects of herbivores
412 on the producer level with increasing plant diversity in the studied forest stands (see also
413 Rudolf 2012).

414 The increase in herbivore biomass and abundance which we found differs from recent
415 studies in grasslands that reported no significant effects of plant phylogenetic diversity on
416 herbivore abundance patterns (in contrast to stronger effects on herbivore species richness;
417 Dinnage et al. 2012; Pellissier et al. 2013). However, these studies indicated either a strong
418 top-down control of herbivore abundances by predators (Dinnage et al. 2012) or focused on
419 specialized herbivore taxa (Pellissier et al. 2013). As our results show, predator top-down
420 control seems to be, at best, weak for the arthropod assemblages of woody plant saplings at
421 our study site, and the probable dominance of generalist herbivores may explain deviations
422 from patterns for more specialized taxa.

423 Such deviations between herbivore taxa also became evident to some extent in our
424 study, as we found no significant effect of plant phylogenetic diversity on the biomass of sap-
425 sucking herbivores. Indeed, we did not find sap sucker biomass to be related to any of the plot
426 characteristics. And while the biomass dispersion of sap suckers increased with plant
427 phylogenetic diversity in summer (Time 3), this relationship was not evident in spring and
428 fall, again suggesting an overall much weaker effect of plant diversity on sap suckers as
429 compared to leaf chewers. Differences in feeding mode and in the degree of host
430 specialization could have caused these feeding guild-specific results, but the ultimate drivers
431 are difficult to elucidate with our study. Nevertheless, several studies that included sap
432 suckers in their analyses likewise found no or only weak direct effects of plant diversity
433 measures on these herbivores (e.g. Koricheva et al. 2000; Unsicker et al. 2006; Vehviläinen et
434 al. 2007). As sap suckers pierce plants to consume assimilates from phloem, xylem, or
435 individual cells, they trigger different signaling pathways in plants and are able to avoid many

436 of the morphological and chemical defense mechanisms that deter leaf chewers (Howe and
437 Jander 2008; Zvereva et al. 2010) and that may be related to the phylogenetic structure and
438 diversity of plant communities (Baraloto et al. 2012). This may weaken potential relationships
439 with plant phylogenetic diversity for sap-sucking herbivores and explain the patterns we
440 found in our study, especially if a dominance of leaf chewers shifts plant responses to a
441 stronger defense against these dominant herbivores (see also Carmona and Fornoni 2013).
442 Analyses at the level of individual arthropod species might potentially provide
443 further insight, but are beyond the scope of our study. Moreover, as most herbivores show at
444 least some degree of lineage-specificity in their host use (Weiblen et al. 2006), and
445 considering that we sampled a wide range of woody plant species in each of our plots and
446 analyzed mean values for arthropods averaged across all woody plant individuals sampled per
447 plot, it is unlikely that our results are driven by the response of only a few specific arthropod
448 species from specific woody plant species. Rather, the overall changes in biomass point to
449 more general effects across larger parts of the herbivore assemblages. This is supported by our
450 finding that the biomass distribution (Q_{Bio}) of leaf chewers increased with woody plant
451 phylogenetic diversity, indicating that a wider range of species of different body size were
452 promoted.
453
454 *Predators and the predator-herbivore ratio*
455 In contrast to herbivores feeding directly on plants, organisms at higher trophic levels are less
456 strongly related to the plant community. The impact of plant diversity may thus be expected
457 to become weaker higher up in food webs (Scherber et al. 2010). However, several recent
458 studies have shown that predator abundance can strongly increase with plant diversity and
459 particularly also with plant phylogenetic diversity (e.g. Haddad et al. 2009; Dinnage et al.
460 2012). This may occur either through positive bottom-up effects of the quantity of available
461 prey resources or via increased structural and non-trophic components of more diverse plant

462 communities (Root 1973; Haddad et al. 2009). While our study indicates that predator
463 abundance (but not biomass) was positively related to herbivore abundance, the strong effects
464 of plant phylogenetic diversity on the latter did not translate to the predator level. The lack of
465 plant phylogenetic diversity effects might be due to the fact that generalist predators
466 (predominantly spiders), which may be less responsive to effects of plant phylogeny on
467 herbivore assemblage structure than specialized predators, made up the largest proportion of
468 both total predator biomass and abundance. Moreover, considering that the diet of generalist
469 predators is made up of various herbivore guilds, the lack of a plant phylogenetic diversity
470 effect on sap suckers may have contributed to suppressing an overall plant diversity effect on
471 predators.

472 Overall, these patterns indicate that predators exert weak top-down control on
473 herbivore biomass and abundance in the undergrowth of the studied forest stands, and that
474 bottom-up effects of the producer level prevail. This is also supported by the decreasing ratios
475 of predator to herbivore biomass and abundance with increasing plant phylogenetic diversity
476 and woody plant species richness. With regard to plant diversity-dependent regulation
477 mechanisms of ecosystem functions, this suggests that the often hypothesized strong
478 mediating role of higher trophic levels for such species-rich forests (Schemske et al. 2009;
479 Terborgh 2012) in our case particularly applies to dominant herbivores and less so to
480 predators or less abundant herbivores. As our study focused on tree and shrub recruits rather
481 than on the established canopy tree community, these patterns may have strong effects on the
482 long-term structuring of the woody plant communities. Our previous studies showed that
483 saplings of abundant tree and shrub species experienced greater damage than less common
484 species and that this damage increased with woody plant diversity (Schuldt et al. 2010;
485 Schuldt et al. 2012). The higher biomass and abundance of herbivores in the more diverse
486 forest stands may thus actually contribute to maintaining this high plant diversity, by
487 decreasing the performance of common tree and shrub species, and thus promoting

coexistence with less common species (see also Dyer et al. 2010).

Conclusions

The strong effects of woody plant phylogenetic diversity, and the much less pronounced direct effects of plant species richness, on herbivore biomass and abundance show that the diversity-dependence of ecosystem processes and interaction pathways across trophic levels can fundamentally depend on non-random associations among species. Scenarios of random species loss may thus underestimate the consequences for ecosystem functions if they do not reflect the driving forces of community assembly (see also Dinnage et al. 2012). Our study particularly highlights the impact of strong bottom-up effects of plant phylogenetic diversity, whereas top-down effects of predators, at least for the undergrowth of tree and shrub recruits studied here, are less responsive to plant diversity and in this context exert weak effects on herbivores. However, this means that herbivores may, in turn, strongly impact particular plant species, which may potentially lead to a positive feedback loop of bottom-up controlled herbivores on plant diversity maintenance. Moreover, considering that biomass is directly related to metabolic rates and the performance of individuals (Saint-Germain et al. 2007; Reiss et al. 2011), the more pronounced effects of plant diversity on arthropod biomass than on abundance found in our study suggest that abundance patterns alone (although more frequently analyzed than biomass patterns in ecological studies; Reiss et al. 2011) may be less effective in capturing the diversity-dependent impact of arthropods in such species-rich ecosystems.

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519

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Table 1. Mixed-effects models for the biomass of leaf-chewing herbivores, sap-sucking herbivores, predators, and the biomass ratio of predators to herbivores across 27 forest stands in subtropical China. Parameter estimates (with standard errors, degrees of freedom, t and *P* values) are shown for the variables retained in the minimal models

	Herbivores: Leaf chewers					Herbivores: Suckers					Predators					Predator : Herbivore ratio				
Fixed effects[a,b]	Est.	*SE*	*DF*	t	*P*	Est.	*SE*	*DF*	t	*P*	Est.	*SE*	*DF*	t	*P*	Est.	*SE*	*DF*	t	*P*
Intercept	1.53	0.14	52	10.6	<0.001	-0.64	0.23	52	-2.8	0.007	1.40	0.06	54	23.0	<0.001	-0.40	0.16	52	-2.5	0.016
Time 2-1[c]	0.61	0.19	52	3.2	0.003	1.40	0.32	52	4.3	<0.001	-	-	-	-	-	-0.47	0.22	52	-2.2	0.035
Time 3-1[c]	*0.26*	*0.19*	*52*	*1.3*	*0.183*	*-0.51*	*0.32*	*52*	*-1.6*	*0.122*	-	-	-	-	-	*-0.05*	*0.22*	*52*	*-0.2*	*0.825*
Plot age	-	-	-	-	-	-	-	-	-	-	0.17	0.06	25	2.8	0.009	-	-	-	-	-
Woody plant species richness (log)	*0.18*	*0.10*	*24*	*1.9*	*0.067*	-	-	-	-	-	-	-	-	-	-	*-0.18*	*0.10*	*23*	*-1.8*	*0.093*
Qphyl s.e.s.[c]	0.21	0.10	24	2.3	0.033	-	-	-	-	-	-	-	-	-	-	-0.28	0.12	23	-2.4	0.026
Woody plant richness : *Qphyl* s.e.s.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.30	0.13	23	2.4	0.025
AICc full model[d]	205.4					298.1					153.9					231.4				
AICc min. model[d]	192.4					266.0					127.5					206.9				

[a]Sapling height, elevation, and the interactions *Qphyl* s.e.s : plot age, richness : plot age, time : *Qphyl* s.e.s , time : plot age, and time : richness were included in the full models but not retained in any of the minimal models

[b]Italics denote data for non-significant terms retained in the minimal models

[c]*Qphyl* s.e.s. = standardized effect sizes of woody plant phylogenetic diversity (*Qphyl*)

[d]Akaike information criterion (corrected for small sample sizes) of the full model (containing all predictors) and the minimal adequate model (simplified model with lowest AICc)

Table 2. Mixed-effects models for the functional dispersion (Q_{Bio}) of the biomass of leaf chewer, sap-sucker, and predator individuals per plot across 27 forest stands in subtropical China. Parameter estimates (with standard errors, degrees of freedom, t and *P* values) are shown for the variables retained in the minimal models

	Herbivores: Leaf chewers					Herbivores: Suckers					Predators				
Fixed effects[a,b]	Est.	*SE*	*DF*	t	*P*	Est.	*SE*	*DF*	t	*P*	Est.	*SE*	*DF*	t	*P*
Intercept	-3.58	0.05	54	-75.4	<0.001	-4.25	0.21	50	-20.5	<0.001	-2.28	0.03	50	-72.2	<0.001
Time 2-1[c]	-	-	-	-	-	0.73	0.29	50	2.5	0.016	*0.07*	*0.04*	*50*	*1.5*	*0.148*
Time 3-1[c]	-	-	-	-	-	*0.43*	*0.29*	*50*	*1.5*	*0.149*	0.18	0.04	50	4.0	<0.001
Plot age	*0.09*	*0.05*	*22*	*2.0*	*0.058*	-	-	-	-	-	-	-	-	-	-
Woody plant species richness (log)	0.12	0.05	22	2.4	0.024	-	-	-	-	-	*0.05*	*0.03*	*25*	*1.4*	*0.166*
Qphyl s.e.s.	0.19	0.06	22	3.4	0.003	*-0.06*	*0.21*	*25*	*-0.3*	*0.759*	-	-	-	-	-
Woody plant richness : *Qphyl* s.e.s.	-0.15	0.06	22	-2.5	0.022	-	-	-	-	-	-	-	-	-	-
Time 2 : *Qphyl* s.e.s.	-	-	-	-	-	*-0.04*	*0.29*	*50*	*-0.1*	*0.890*	-	-	-	-	-
Time 3 : *Qphyl* s.e.s.	-	-	-	-	-	0.67	0.29	50	2.3	0.027	-	-	-	-	-

Time 2 : Woody															
plant richness	-	-	-	-	-	-	-	-	-	-	-0.11	0.04	50	-2.5	0.014
Time 3 : Woody															
plant richness	-	-	-	-	-	-	-	-	-	-	-0.07	0.04	50	-1.6	0.108
AICc full model	116.5					281.5					-24.4				
AICc min. model	88.4					253.1					-51.2				

[a]Sapling height, elevation, and the interactions *Qphyl* s.e.s : plot age, richness : plot age, and time : plot age were included in the full models but not retained in any of the minimal models

[b]Italics denote data for non-significant terms retained in the minimal models

[c]*Qphyl* s.e.s. = standardized effect sizes of woody plant phylogenetic diversity (*Qphyl*)

[d]Contrasts between sampling time 1 (fall) and the successive sampling times 2 and 3 (spring and summer); the intercept is the overall mean

[e]Akaike information criterion (corrected for small sample sizes) of the full model (containing all predictors) and the minimal adequate model (simplified model with lowest AICc)

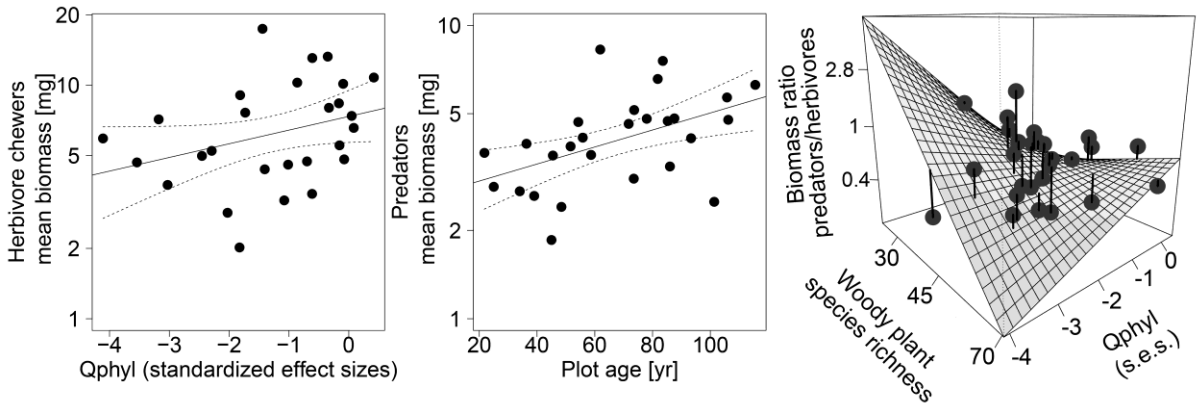

Figure 1. Relationships between woody plant phylogenetic diversity (Q_{phyl} s.e.s.), woody plant species richness, plot age and the biomass of a) leaf chewers, b) predators, and c) the ratio of predators to herbivores across 27 forest plots in subtropical China. All relationships are significant at $P < 0.05$ (see Table 1 for details).

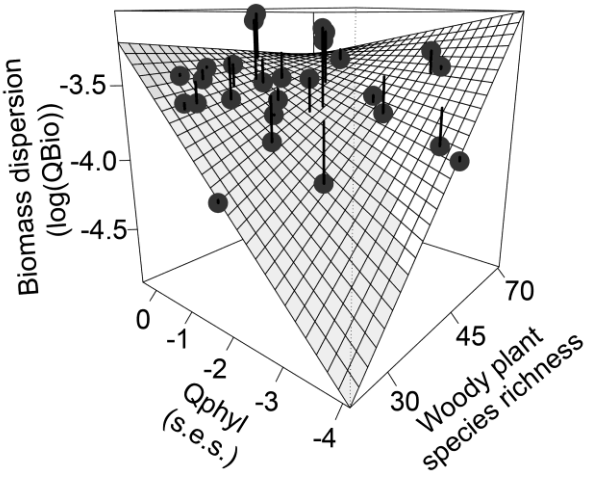

Figure 2. Relationships between the dispersion of biomass per plot among individuals of leaf-chewing herbivores and woody plant phylogenetic diversity (Q_{phyl} s.e.s) and woody plant species richness. All relationships are significant at $P < 0.05$ (Table 1).